SOCIAL LIFE AMONG THE INSECTS[1]

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LECTURE II. PART 2. WASPS SOLITARY AND SOCIAL

Authorities on the classification of the social wasps now divide them into five subfamilies, namely the Stenogastrinæ, which are confined to the Indomalayan and Australian Regions, the Ropalidiinæ, confined to the tropics of the Old World, the Polistinæ, which are cosmopolitan, the Epiponinæ, possibly comprising two independent lines of descent from Eumenes-like and Odynerus-like ancestors respectively and constituting a large group, mostly confined to tropical America, with a few species in the Ethiopian, Endomalayan, Australian and North American regions, and the Vespinæ, which are recorded from all the continents except South America and the greater portion of Africa south of the Sahara. These five families may be briefly characterized before considering some of the peculiarities of social organization common to most or all of them.

(1). The Stenogastrinæ evidently represent a group of great interest, because they form a transition from the solitary to the social wasps, but unfortunately our knowledge of their habits is very incomplete. F. X. Williams has recently published observations on four Philippine species, and though his account is fragmentary, it nevertheless reveals some peculiar conditions. He shows that the single genus of the subfamily, Stenogaster, includes both solitary and social forms and that all of them exhibit a mixture of primitive and specialized traits. The species all live in dark, shady forests and make very delicate, fragile nests with particles of decayed wood or earth. *S. depressigaster* (Figs. 30 E and F) hangs its long, slender, cylindrical nests to a pendent hair-like fungus or fern. The structure consists of tubular, intertwined galleries and cells, with their openings directed downwards. The colony comprises only a few individuals probably the mother wasp and her recently emerged daughters. The eggs are attached to the bottoms of the cells as in all social wasps and the larvæ are fed from day to day with a gelatinous paste, which Williams believes may be of vegetable origin. In the cells the older larvæ and the pupæ hang head downwards. Another social species, *S. vari-*

[1] Lowell Lectures.

pictus, constructs a very different nest, consisting of cells made of sandy mud mixed perhaps with particles of decayed wood and attached side by side in groups to the surfaces of rocks and tree-trunks (Fig. 30 G). In this case also the cell-openings are directed downward. A nest may consist of thirty or more cells in several

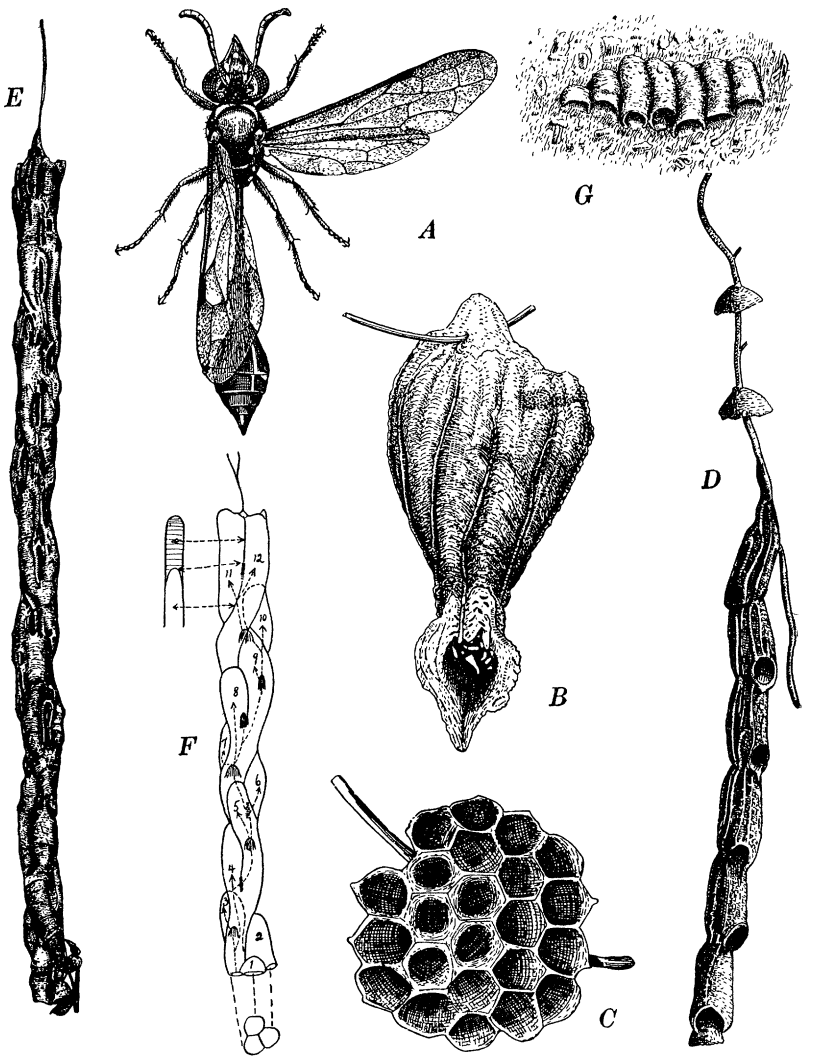

FIG. 30

Nests of Stenogastrine wasps from the Philippines. *A. Stenogaster micans* var. *luzonensis,* female. *B.* Completed nest of same; *C.* Nest with only the basal portion completed; *D.* Nest of *Stenogaster* sp., with umbrella-like "guards"; *E.* Nest of *S. depressigaster; F.* diagram of same showing arrangement of cells and passage-ways. The numbers indicate the cells. The tops of the passage-ways are shown in two planes by series of parallel lines. *G.* Nest of *S. varipictus* on the bark of a tree. (After F. X. Williams).

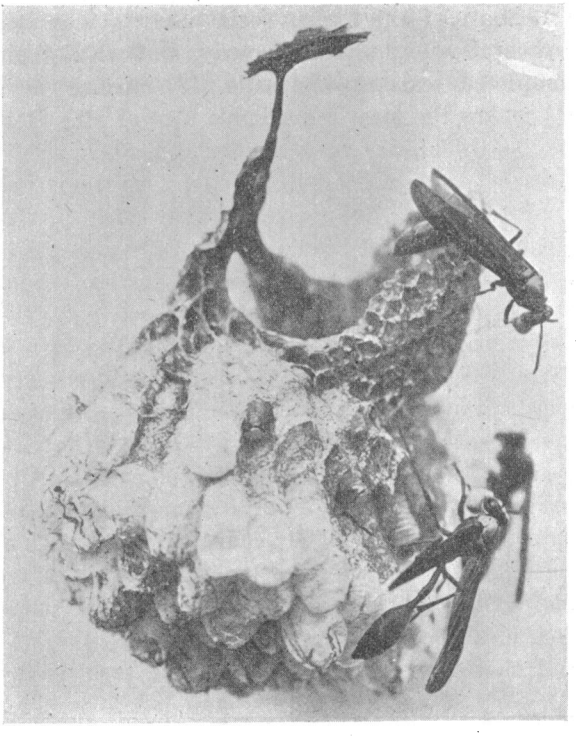

FIG. 31

Suspended and naked comb of a very primitive African Epiponine wasp, *Belonogaster junceus,* with young cells above and old cells containing larvæ below; natural size. Most of the wasps have been removed but two are seen bringing food-pellets to the larvæ. (Photograph by E. Roubaud).

rows. There are only a few wasps in a colony, and when the larvæ are full-grown the cells are sealed up by the mother as in the solitary wasps. But after the young have emerged the cells may be used again as in many of the social species. Williams describes and figures the nests of two solitary species, one an undetermined form, the other identified as *S. micans* var. *luzonensis.* The nest of the former (Fig. 30 D) is suspended, like that of *depressigaster,* from some thin vegetable fibre and appears to consist of particles of decayed wood. It is a beautiful, elongate structure of seven tubular, ribbed cells, arranged in a zigzag series with their openings below and two peculiar umbrella-like discs around the supporting fibre. These discs "remind one a good deal of the metal plates fastened to the mooring lines of vessels and serving as rat guards. Their function in the case of the nest may be an imperfect protection from the ants, or perhaps they may serve as umbrellas, though neither they nor the cells are strictly rain proof." They may possibly be rudiments of the nest envelopes which are so elaborately

developed in many of the higher social wasps. The mother wasp attends to several young simultaneously, and when their development is completed seals up the cells. *S. micans* var *luzonensis* (Fig. 30 B) makes the most remarkable nest of all. It is attached to some pendent plant filament under an overhanging bank or under masses of dead leaves supported by twigs or vines and is made of "moist and well-decayed wood chewed up into a pulp and formed into delicate paper which is not rain proof." The basal portion of the nest (Fig. 30 C) is a single comb of about 20 regular, hexagonal cells, enclosed in a pear-shaped covering which is longitudinally grooved and ribbed on the outside and constricted below to form a filigree-work, funnel-like aperture surrounded on one side by a spear-shaped expansion. This species seems also to have been observed in Ceylon by E. E. Green, who remarks that "the nest seems to be the property of one pair only" of wasps. Two other species, *S. nigrifrons* of Burma and *melleyi* of Java, are also recorded as social. They make nests consisting of a few pendent, hexagonal-celled combs attached to one another by slender pedicels. All of the descriptions indicate that the colonies of the social species of Stenogaster must consist of very few individuals, and there is nothing to show that the female offspring

FIG. 32

Nest of *Polybioides tabida* from the Congo, with the involucre partly removed. (After J. Bequaert from a photograph by H. O. Lang).

differ in any way from their mother or that they assist in caring for the brood. Even in the case of *S. varipictus,* Williams remarks: "In a small way, it seems to be a social wasp; one to several insects

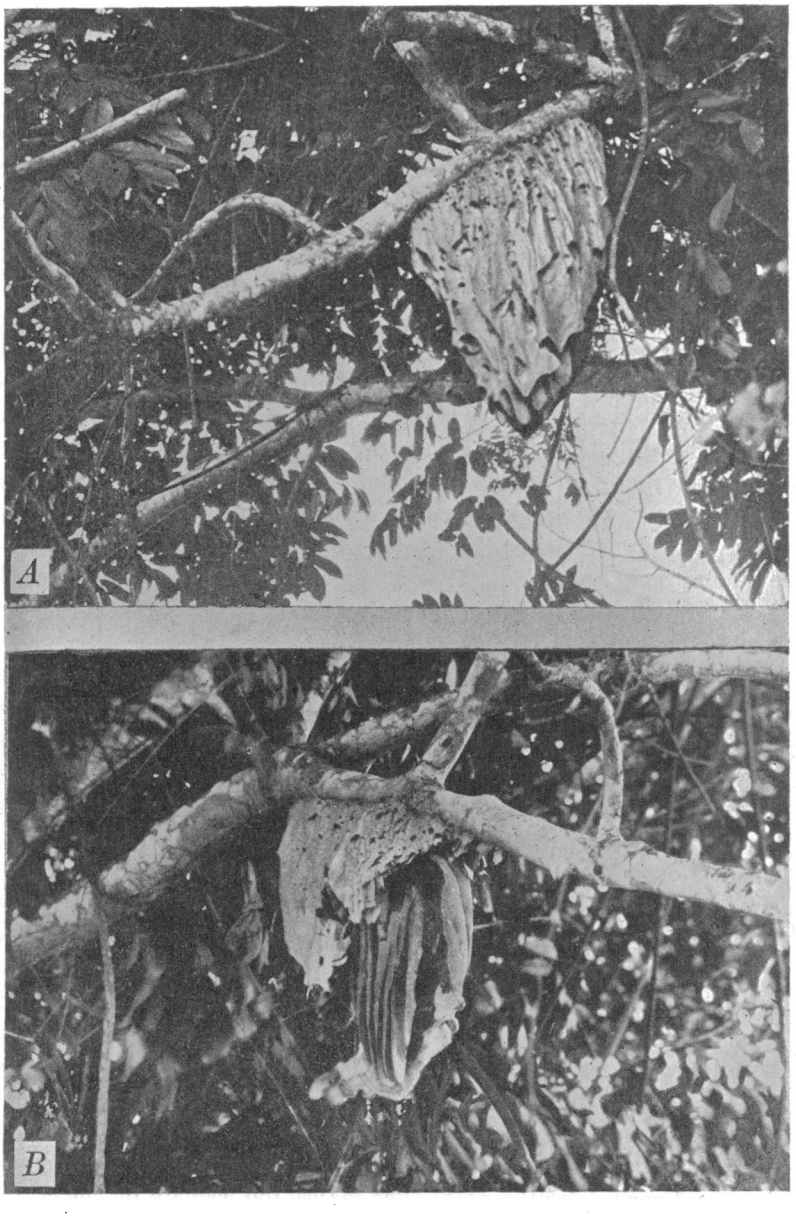

FIG. 33

A. Nest of *Polybioides melaena* of the Congo. *B.* The same partly destroyed, showing the pendent combs, which have cells on both sides. (After J. Bequaert, from a photograph by H. O. Lang).

attend to a cell group. It may be, however, that each female has her own lot of cells in this cell group.'' Future investigations may show that none of the species of Stenogaster is really social in the same sense as are the four other subfamilies, though they approach the definitively social forms in using paper in the construction of the nest, in sometimes making combs of regular hexagonal cells and in caring for a number of larvæ at the same time.

(2). The Epiponinæ are a large and heterogeneous group, comprising a much greater number of genera (23) than any other subfamily of social wasps, and ranging all the way from very primitive forms like Belonogaster to highly specialized forms like Chartergus and Nectarina. Great differences are also apparent in the architecture of the nest, which in the more primitive genera consists of a single naked comb of hexagonal cells attached to some support by a peduncle (Fig. 31), and in the more advanced forms of a single comb or of several combs superimposed on one another and enclosed in an envelope with an opening for ingress and egress (Figs. 32 and 33). The combs are in some cases pedunculate (stelocyttarous), in others attached directly to the support or to the envelope (phragmocyttarous). In nearly all cases the nest is made entirely of paper, but in a few tropical American species some clay may be added. It is always above ground and attached to the branches or leaves of trees, to the underside of some shelter (roofs, banks, etc.). In primitive forms like Belonogaster (Fig. 31), as a rule, a single fecundated female starts the nest by building a single pedunculate cell and then gradually adding others in circles concentrically to its periphery as the comb grows, but not infrequently the foundress may be joined by other females before the work has progressed very far. Each larva is fed with pellets of malaxated caterpillars till it is full grown when it spins a convex cap over the orifice of its cell and pupates. The emerging females are all like the mother in possessing well-developed ovaries and in being capable of fecundation. In other words, all the females of the colony are physiologically equal, and even such differences in stature as they may exhibit have no relation to fertility. The colonies are small, the nests having usually only about 50 to 60 cells, rarely as many as 200 to 300. In larger colonies there is a certain rude division of labor since the older females devote themselves to egg-laying, the younger to foraging for food and nest materials and the recently emerged individuals to feeding the larvæ and caring for the nest. The males, too, remain on the comb, but behave like parasites and exact food whenever it is brought in by the foraging females. Belonogaster is described as a polygynous wasp because each of its colonies contains a number

of fecundated females. When it has reached its full development the females leave in small companies and found new nests either singly or together. This phenomenon is known as "swarming" and occurs only in the wasps of the tropics where it seems to be an adaptation to the favorable climatic conditions. In the higher South American genera of Epiponinæ, however, the females are not all alike but are differentiated into true females, or queens, *i. e.,* individuals with well-developed ovaries and capable of fecundation, and workers, *i. e.,* females with imperfectly developed ovaries and therefore sterile or capable only of laying unfertilized, male-producing eggs. Many of these wasps, according to H. and R. von Ihering and Ducke, are polygynous and regularly form new colonies and nests by sending off swarms of workers with one or two dozen queens. The colonies often become extremely populous and comprise hundreds or even thousands of individuals. Some of the species (Nectarina, Polybia) have a habit of storing a considerable amount of honey in their combs, while others are known to capture, kill and store within the nest envelope, and even in the combs, quantities of male and female termites or male ants as a supply of food to be drawn on when needed.

(3). The Ropalidiinæ are a small group of only three genera, the best known of which is Ropalidia. These are primitive wasps which build a single naked comb like that of Belonogaster and feed their young with pellets of malaxated insects. The colonies are small and polygynous, but, according to Roubaud, true workers can be distinguished, though they are few in number compared with the true females. Swarming seems to occur in some species.

(4). The Polistinæ are represented by only two genera. One of these, Polistes, is cosmopolitan and, like Ropalidia and Belonogaster, makes a single, naked comb, suspended by a central or eccentric peduncle to the underside of some shelter. As there are several common species in Europe and the United States, the habits of the genus are well known. The nest is usually established and in its incipient stages constructed by a single female, or queen. A certain number of her offspring are workers though they seem often to lay male-producing eggs. True females are rather numerous in the colonies of some species, which may therefore be regarded as polygynous, and some of the tropical forms may, perhaps, swarm. In temperate regions, however, the Polistes colony is an annual development and usually not very populous. The young females are fecundated in the late summer and pass the winter hidden away under bark or in the crevices of walls, whence they emerge in the spring to found new colonies. Several of the species, even in temperate regions, are known to store small quantities of honey in their combs.

(5). Like the Polistinæ, the subfamily Vespinæ includes only two genera, Vespa and Provespa. The species of the former, the only genus besides Polistes that occurs in the north temperate zone, are the largest and most typical of social wasps. So far as known the species are strictly monogynous. The nest, founded by a single female, consists at first of a small pendent comb, like that of Polistes, but while there are still only a few cells a more or less spherical envelope is built around it. The eggs first laid produce workers, which are much smaller than the mother and incapable of fecundation. They remain with the parent, enlarge the comb and envelope and, to accommodate the rapidly increasing brood, build additional combs in a series from above downward, each new comb being supported by one or more peduncles attached to the comb above it (stelocyttarous). At first large numbers of workers are produced, but later in the summer males and females appear. Owing to the greater size of the females, the cells in which they are reared are considerably larger than the worker cells. After the mating of the males and females the colony perishes, with the exception of the fecundated females, which hibernate like the females of Polistes and during the following spring found new colonies. In the Vespinæ, therefore, a very distinct worker caste has been developed, though its members occasionally and perhaps regularly lay male-producing eggs. The species of Vespa are usually divided into two groups, one with long, the other with very short cheeks. In Europe and North America the long-cheeked forms as a rule build aerial nests above ground, the short-cheeked forms in cavities which they excavate in the ground. The colonies may often be very populous by the end of the summer (3,000 to 5,000 individuals).

After this hasty sketch of the five subfamilies of the social wasps we may consider a few of their fundamental behavioristic peculiarities, especially the trophic relations between the adults and larvæ, the origin of the worker caste, its ultimate fate in certain parasitic species and the question of monogyny and polygyny. In all these phenomena we are concerned with effects of the food-supply and therefore of the external environment.

The feeding of the larvæ by Vespa and Polistes queens and workers with pellets made of malaxated portions of caterpillars, flies or other insects has often been described and can be readily witnessed in any colony kept in the laboratory. The hungry larvæ protrude their heads with open mouths from the orifices of the cells, like so many nestling birds, and when very hungry may actually scratch on the walls of the cells to attract the attention of the workers or their nurses. The feeding is not, however, a one-sided

affair, since closer observation shows that the wasp larva emits from its mouth drops of sweet saliva which are eagerly imbibed by the nurses. This behavior of the larvæ has been observed in all four subfamilies of the higher wasps by du Buysson, Janet and Roubaud. Du Buysson says that the larvæ of Vespa "secrete from the mouth an abundant liquid. When they are touched the liquid is seen to trickle out. The queen, the workers and the males are very eager for the secretion. They know how to excite the offspring in such a way as to make them furnish the beverage." And Janet was able to prove that the secretion is a product of the salivary or spinning glands and that it flows from an opening at the base of the lower lip. "This product," he says, "is often imbibed by the imagines, especially by the just emerged workers and by the males, which in order to obtain it, gently bite the head of the larva." Most attention has been bestowed on this reciprocal feeding by Roubaud, from whose interesting account of Belonogaster, Ropalidia and Polistes I take the following paragraphs:

"All the larvæ from birth secrete from a projection of the hypopharynx, on the interior surface of the buccal funnel, an abundant salivary liquid, which at the slightest touch spreads over the mouth in a drop. All the adult wasps, males as well as females, are extremely eager for this salivary secretion, the taste of which is slightly sugary. It is easy to observe, especially in Belonogaster, the insistent demand for this larval product and the tactics employed to provoke its secretion.

"As soon as a nurse wasp has distributed her food pellet among the various larvæ, she advances with rapidly vibrating wings to the opening of each cell containing a larva in order to imbibe the salivary drop that flows abundantly from its mouth. The method employed to elicit the secretion is very easily observed. The wing vibrations of the nurse serve as a signal to the larva, which, in order to receive the food, protrudes its head from the orifice of the cell. This simple movement is often accompanied by an immediate flow of saliva. But if the secretion does not appear the wasp seizes the larva's head in her mandibles, draws it toward her and then suddenly jams it back into the cell, into which she then thrusts her head. These movements, involving as they do a stimulation of the borders of the mouth of the larva, compel it to secrete its salivary liquid.

"One may see the females pass back and forth three or four times in front of a lot of larvæ to which they have given nutriment, in order to imbibe the secretion. The insistence with which they perform this operation is such that there is a flagrant disproportion between the quantity of nourishment distributed among the larvæ

by the females and that of the salivary liquid which they receive in return. There is therefore actual exploitation of the larvæ by the nurses.

"The salivary secretion may even be demanded from the larva without a compensatory gift of nourishment, both by the females that have just emerged and by the males during their sojourn in the nest. The latter employ the same tactics as the females in compelling the larvæ to yield their secretion. They demand it especially after they have malaxated an alimentary pellet for themselves, so that there is then no reciprocal exchange of nutritive material.

"It is easy to provoke the secretion of the larvæ artificially. Merely touching the borders of the mouth will bring it about. The forward movement of the larvæ at the cell entrance, causing them to protrude their mouths to receive the food pellet, is also easily induced by vibrations of the air in the neighborhood of the nest. It is only necessary to whistle loudly or emit shrill sounds near a nest of Belonogaster to see all the larvæ protrude their heads to the orifice of the cells. Now it is precisely the vibrations of the air created by the rapid agitation of the bodies of the wasps and repeated beating of their wings that call forth these movements, either at the moment when food is brought or for the purpose of obtaining the buccal secretion which is so eagerly solicited."

Roubaud has called the interchange of food here described "oecotrophobiosis," but for reasons which I cannot stop to discuss, I prefer to use the word "trophallaxis." It will be seen that the larvæ have acquired a very definite meaning for the adult wasps of all the castes and that through trophallaxis very close physiological bonds have been established, which serve to unite all the members of the colony, just as the nutritive blood stream in our bodies binds all the component cells and tissues together. We found that even in forms like *Synagris cornuta* the larva has acquired a meaning for the mother. In this case Roubaud has shown that the mother while malaxating the food-pellet herself imbibes its juices before feeding it to the larva, and that "the internal liquids having partly disappeared during the process of malaxation, the prey is no longer, as it was in the beginning, soft and juicy and full of nutriment for the larva. It is possible, in fact, to observe that the caterpillar *pâté* provided by the *Synagris cornuta* is a coarse paste which has partly lost its liquid constituents. There is no exaggeration in stating that such food would induce in larvæ thus nourished an increase of the salivary secretion in order to compensate for the absence of the liquid in the prey and facilitate its digestion." It is here that the further development to the condition

seen in Belonogaster and other social wasps sets in. The mother finds the saliva of the larva agreeable and a trophallactic relationship is established. As Roubaud says, "the nursing instinct having evolved in the manner here described in the Eumenids, the wasps acquire contact with the buccal secretion of the larva, become acquainted with it and seek to provoke it. Thence naturally follows a tendency to increase the number of larvæ to be reared simultaneously in order at the same time to satisfy the urgency of oviposition and to profit by the greater abundance of the secretion of the larvæ."

As I shall endeavor to show in my account of the ants and termites, trophallaxis is of very general significance in the social life of insects. It seems also to have an important bearing on the development of the worker caste. Both queens and workers arise from fertilized eggs, and the differences between them are commonly attributed to the different amounts of food they are given as larvæ. There seems to be much to support this view in the social wasps. As Roubaud points out in the passages quoted, the larvæ are actually exploited by the adult wasps to the extent of being compelled to furnish them with considerable quantities of salivary secretion, often out of all proportion to the amount of solid food which they receive in return. Owing to this expenditure of substance and the number of larvæ which are reared simultaneously, especially during the earlier stages of colony formation, they are inadequately nourished and have to pupate as rather small individuals, with poorly developed ovaries. Such individuals therefore become workers. This inhibition of ovarial development, which has been called "alimentary castration," is maintained during the adult life of most workers by the exigencies of the nursing instincts. The workers have to complete and care for the nest, forage for food and distribute most of it among their larval sisters. All this exhausting labor on slender rations tends to keep them sterile. In other words, "nutricial castration" (derived from *nutrix, a nurse,* to use Marchal's terms, takes the place in the adult worker of the alimentary castration to which it was subjected during its larval period. It is only later in the development of the colony, when the number of workers and consequently also the amount of food brought in have considerably increased, and the labor of foraging and nest construction have correspondingly decreased for the individual worker, that the larvæ can be more copiously fed and develop as fertile females, or queens. At that season, too, some of the workers may develop their ovaries, but as the members of the worker caste are incapable of fecundation, they can lay only male-producing eggs. That this is not the

whole explanation of the worker caste will appear when we come to consider the much more extreme conditions in the ants and termites, but it may suffice to explain the conditions in the social wasps and social bees.

Parasitism is another phenomenon which seems to indicate that a meager or insufficient diet is responsible for the development of the worker caste. Although parasitic species are much more numerous among the bees and ants, I will stop to consider very briefly a few of those known to occur among the wasps. A parasite is, of course, an organism that is able to secure abundant nourishment for itself or its offspring by appropriating the food-supply that has been laboriously stored or assimilated by some other organism. The various parasitic solitary wasps, such as the species of Ceropales, among the spider-storing Psammocharidæ, all substitute their own young for the young of their hosts in order that the larvæ may come into undisputed possession of the stored provisions. Among the social wasps there are only two parasitic species, *Vespa austriaca* and *V. arctica*. The former has long been known in Europe where it lives in the nests of *V. rufa*. Recently Bequaert and Sladen have found *austriaca* in the United States, British America and Alaska, but its Cisatlantic host is still unknown, though believed to be *V. consobrina*. *V. arctica*, as Fletcher, Taylor and I have demonstrated, lives in the nests of our common yellow jacket (*V. diabolica*). Now both *austriaca* and *arctica* have completely lost the worker caste so that they are represented only by males and fertile females. They were at one time undoubtedly non-parasitic like their present hosts, but are now reared and fed by the workers of the latter like their own more favored sexual forms. As a result of such nurture what were once independent social insects with two female forms have actually reverted to the status of solitary forms with only one type of female.

In conclusion the conditions of monogyny and polygyny in the higher social wasps may be briefly considered. It was shown that the Vespinæ and at least most of the Polistinæ are monogynous, their colonies being annual developments begun by a single fecundated queen, and that they perish at the end of the season, with the exception of the annual brood of queens, which after fecundation hibernate and start new colonies during the following spring. Many of the tropical Epiponinæ and Ropalidiinæ, however, are polygynous and the former often form large perennial colonies which from time to time send off swarms consisting of numerous fecundated females or of such females accompanied by workers to found new colonies. This behavior is evidently as perfect an adaptation to the continuously favorable food and temperature condi-

tion of the tropics as is that of Vespa and Polistes to the pronounced seasonal vicissitudes of the temperate regions. There has been a difference of opinion among the authorities as to whether monogyny or polygyny represents the more primitive phylogenetic stage among the social wasps. The great majority of these insects are tropical, and probably even Vespa and Polistes were originally inhabitants of warm regions and invaded temperate Eurasia and North America during postglacial times. The monogyny still exhibited by these wasps in the tropics may have been acquired there as an adaptation to the wet and dry seasons, and this adaptation may have enabled them the more easily to adjust themselves to the warm and cold seasons of more northern regions. H. and R. von Ihering and Roubaud may therefore be right in maintaining that polygyny is the more primitive condition. Their view is also supported by the fact that in the polygynous genera the worker caste is either still absent (Belonogaster) or very feebly developed and constitutes only a small percentage of the female personnel of the colony. We might, perhaps, say that our species of Vespa and Polistes each year produce a swarm of females and workers but that the advent of cold weather destroys the less resistant workers and permits only the dispersed queens to survive and hibernate till the following season.

We shall find precisely the same differences between monogyny and polygyny in the social bees of temperate and tropical regions, and somewhat analogous conditions among the ants, although their polygyny may be secondarily derived from monogyny. It would seem that swarming must be a phenomenon which occurs as a rule when the environment is unfavorable or the colony has grown to such dimensions as to outrun its food-supply so that emigration of portions of its population becomes imperative.